Nectarivorous bats as pollinators of trees in West Malaysia

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In West Malaysia three species of truly nectarivorous bats occur commonly in suitable localities. They differ greatly in their roosting habits and/or food sources and there is little ecological overlap. *Eonycteris spelaea* Dobson roosts in large colonies in caves, travels considerable distances to feed, forages in flocks, and obtains most of its food from a wide diversity of scattered, seasonally flowering sources. In contrast *Macroglossus minimus* (Geoffroy) and *M. sobrinus* (Andersen) roost singly or in well spaced groups in trees close to their major food sources (*Sonneratia* species for *M. minimus*, *Musa* spp. for *M. sobrinus*), forage singly, and obtain most of their food from a few gregarious, aseasonally flowering sources. The feeding habits of all three species allow them to act as successful pollinators. Their role as pollinators of certain economically important trees is discussed, further studies suggested, and the importance of conservation emphasized.

CONTENTS

INTRODUCTION

In recent years there has been an increasing interest in animal-plant interactions in the tropics and the importance of animals as pollen vectors in tropical regions is now fairly well documented (e.g. Frankie, Baker & Opler, 1974a). The majority of pollen vectors are insects but for a long time it has been known that certain bats (Chiroptera) are capable of pollinating some economically important plants (e.g. Hart, 1897). The Chiroptera are divisible into two suborders: the Megachiroptera are exclusively Old World and principally frugivorous; the Microchiroptera occur in both Old and New Worlds and are largely insectivorous, although a few New World species are at least partly frugivorous. A few members of both suborders have adopted a diet of nectar and pollen, and can pollinate the flowers upon which they feed.

To date, the most significant studies of chiropterophily, the association of bats with flowers, have occurred with the Microchiroptera of the New World (e.g. Alvarez & Quintero, 1970; Baker, 1970b, 1973; Frankie *et al.*, 1974a; Heithaus, Opler & Baker, 1974; Howell, 1974; Vogel, 1968–69). The flower-visiting Megachiroptera of the Old World have been studied largely in Africa (e.g. Ayensu, 1974; Baker & Harris, 1957, 1959; Harris & Baker, 1958, 1959; Jaeger, 1954; Kock, 1972). The first detailed study in Asia was the pioneer study of chiropterophily by van der Pijl (1936) in Java. He later added to and revised this work (van der Pijl, 1941, 1956) but few observations relating to South-east Asia have since been published. Baker & Harris (1957) summarized the early Javanese records quoted by van der Pijl (1936). Nur (quoted from Pursglove, 1972) confirmed that Manila hemp, *Musa textilis* Née, was pollinated by bats in Java. Berwick (1950) published a photograph of the bat *Eonycteris spelaea* Dobson (misidentified as *Cynopterus brachyotis*) visiting the flowers of the silk-cotton tree *Ceiba pentandra* (L.) Gaertn. but did not mention its possible role as pollinator (Baker & Harris, 1959). Both Tan (1965) and Lim (1973) reported pollen in the stomachs of bats of the genus *Macroglossus*.

In West Malaysia three species of the subfamily Macroglossinae (Megachiroptera: Pteropidae) occur, all being fairly widely distributed in South-east Asia: *Eonycteris spelaea*, *Macroglossus minimus* (Geoffroy) and *Macroglossus sobrinus* (Andersen) (Medway, 1969; for a revised taxonomy of *Macroglossus* see Start, 1974). The two species of *Macroglossus* are small (*M. minimus* 16–24 g, *M. sobrinus* 18–26 g) but *E. spelaea* is a medium sized bat (40–70 g). Macroglossinae are distinguished from other Pteropidae by adaptations to a diet of nectar and pollen, especially by the presence of long filiform papillae on the distal portion of the tongue. Although other species of West Malaysian bats, all Pteropidae, are known to be associated with flowers it is apparently only these three species which play a significant role in pollination. A broad study of the feeding biology in relation to food sources of these three, particularly *E. spelaea* and *M. minimus*, was undertaken between January, 1972, and January, 1974 (Start, 1974). The study took place largely in the states of Perak and Selangor, West Malaysia, notably in the mangroves at Rantau Panjang, at Batu Caves, in a rubber estate near Kajang, and in the inland forest at Ulu Gombak and the Tapah-Ringlet road. Emphasis was placed upon investigating the food sources, foraging methods, roosting habits and seasonality of breeding of the bats, and the distribution, morphology, flowering biology and phenology of the relevant plants. In this paper the role of these bats as pollen vectors is considered.

ROOSTING, MOVEMENT AND FEEDING METHODS

Due to differences in their roosting habits, *E. spelaea* has in the past been thought of as a common bat in contrast to the two species of *Macroglossus*. In fact all three are common in suitable localities, *E. spelaea* occurring from sea level to at least 1800 m in a wide diversity of forest types, *M. sobrinus* occurring again from 0–1800 m in the vicinity of wild bananas, *Musa* spp., and *M. minimus* occurring in mangrove in the vicinity of *Sonneratia* spp. The roosting habits of *E. spelaea* are in distinct contrast to those of *Macroglossus* for it generally roosts in tight groups in large colonies in caves, although they are occasionally found in rock shelters or houses (Medway, 1969); Batu Caves is the only large roost known in Selangor and contains tens of thousands of bats. However, both species of *Macroglossus* roost either alone or in small groups, in which the bats are well separated, in trees in the vicinity of their major food sources (*Sonneratia* spp. for *M. minimus*, *Musa* spp. for *M. sobrinus*). All three tend to use the same roost site repeatedly. All start foraging at about dusk (19.00 hrs), and the maximum activity is generally within the first two hours, although some bats remain active until towards dawn (06.00 hrs). Whereas *Macroglossus* forages alone, *E. spelaea* forages in flocks of usually 5–20 bats though up to 50 have been observed.

The primary function of communal roosting and flock foraging in *E. spelaea* may well be the dissemination of information on the location of widely scattered food sources as has been suggested for birds (Ward & Zahavi, 1973). It is noteworthy that foraging is not always random, as netting and ringing showed that individuals often returned to the same site weeks or months after capture there. This may indicate that they have a precise knowledge of their feeding area. If this is so then, if bats can identify pollen on the fur of others in the roost, they would be able to locate its source without random search. With extensive feeding ranges this would be of great value.

Individuals of *E. spelaea* travel considerable distances each night to feed, and their flight is fast and direct. Guano in Batu Caves contained *Sonneratia alba* J. J. Smith pollen, the nearest source of which was at Rantau Panjang 38 km away. The first individuals of *E. spelaea* to reach Rantau Panjang each night arrived about 1.5 h after dusk (when they start foraging), a reasonable time in which to fly 38 km; this suggests that the range for *E. spelaea* is about 38 km and probably greater. Ringing indicated that bats could return repeatedly to the same area to feed, and on any given night often remained within a confined area for many hours. The examination of pollen taken from netted bats indicated that there was partial segregation of sex and age classes when feeding: males were more frequently found in mangrove areas, females more frequently inland, and subadults remained nearer to the cave than adults. There was also an indication of partial segregation at roost.

Macroglossus individuals roost close to their food sources and do not travel large distances each night to feed. The maximum distance they could travel was not ascertained, but ringing showed that they ranged over at least 2 km. Their flight is slower but more agile than *E. spelaea* and this allows them to enter dense vegetation such as banana groves where *E. spelaea* cannot manoeuvre. Ringing indicated that both species remained in one locality for considerable periods of time and often returned repeatedly to one small area or even one tree to feed.

All three species land on the inflorescences to feed, as is typical of Megachiroptera, and do not hover in front as do many New World nectarivorous Microchiroptera (Baker, 1970a, 1973; Baker & Harris, 1957, 1959; Cockrum & Hayward, 1962; Harris & Baker, 1958, 1959; Hayward & Cockrum, 1971; Jaeger, 1945; Start, 1972; Vogel, 1968–69). Whilst on the flower the bats probe rapidly for nectar and occasionally lick pollen directly from the stamens. However, most pollen is obtained by grooming after visiting flowers, for whilst feeding the bats become dusted with pollen, either liberally over much of their bodies or on the head depending upon the type of flower.

All three species spend a very short time on each inflorescence, leaving within a few seconds to visit other inflorescences on the same or different trees. One result of this rapid movement is that each inflorescence can expect a number of visits from pollen-dusted bats each night: observations on three *Sonneratia caseolaris* (L.) Engl. flowers during the peak feeding period soon after dusk recorded an average of 16 visits by *M. minimus* per flower per hour. The reasons why many types of pollinator move rapidly from flower to flower, usually without exhausting the food supply of any one flower, is a question of considerable interest. Frankie (1976) suggests that territorially-related aggression, other aggressive interactions and group foraging may play an important part. An evolutionary tendency in plants towards shorter periods during which floral rewards were available would encourage such interactions and thus the chance of cross-pollination. It still remains to examine in detail the timing, quality and quantity of floral rewards in West Malaysian chiropterophilous plants.

Table 1. Food sources of nectarivorous bats in West Malaysia (from field observations and faecal samples)

PLANTS		CHIROPTERA		
Family	Species	*E. spelaea*[a]	*M. minimus*[b]	*M. sobrinus*[b]
Musaceae	*Musa malaccensis*	* } Trace[c]		+++
	M. truncata	*		+++
	Musa cultivated	*	+++	+++
Palmae	*Cocos nucifera*	* 1.3	+++	
	Arenga spp.	* Trace		
Anacardiaceae	*Mangifera* spp.	* 0.2	++	
Bignoniaceae	*Oroxylum indicum*	* 0.1		
	Pajanelia longifolia	*		
Bombacaceae	*Bombax valetonii*	* 0.7		
	Ceiba pentandra	* 1.6	+	
	Durio zibethinus	* } 3.4	+	} ?
	D. graveolens	*		
Compositae	(species ?)	* Trace		
Lecythidaceae	*Barringtonia* spp.	* Trace		
Leguminosae	*Parkia javanica*	*		
	P. speciosa	* } 11.1		
	P. singularis	*		
Moraceae	*Artocarpus* spp.	* 27.8		
Myrtaceae	*Eugenia malaccensis*	* 4.3	++	
Rhizophoraceae	*Rhizophora* spp.	* Trace	+	
Sapotaceae	(species ?)	* 1.4		
Sonneratiaceae	*Duabanga grandiflora*	* 30.0		++
	Sonneratia alba	* } 11.7	+++	
	S. ovata	*	+	
	S. caseolaris	* 5.6	+++	
?	T3	* 0.7		
?	T10	* 0.3		
?	T4, T6, T12, T13	* Trace		

NOTES: a. *E. spelaea:* source (*), and % of pollen grains in all Batu Caves guano samples.
b. *Macroglossus* species: source (+) and its importance (+++ important, ++ less important, + rare).
c. *Musa* pollen: pollen breaks down in guano: cultivated *Musa* produces no pollen.

FOOD SOURCES

An indication of food sources was obtained by observation of the flowers of chiropterophilous plants, by netting bats and examining the pollen on their bodies and in their faeces, and (for *E. spelaea*) by the regular collection of guano samples from below roosting sites. Results are given in Table 1.

Eonycteris spelaea

Collections of guano were made weekly from Batu Caves, Selangor, and monthly from Gua Sanding, Perak, and a total of about 200,000 grains identified as far as possible (some to species, some not even to family). A total of 31 pollen types were observed. Of these the 11 most common species (*Durio* spp., *Parkia* spp., *Artocarpus* spp., *Eugenia malaccensis* L., *Duabanga grandiflora* (Roxb. ex DC.) Walp., *Sonneratia* spp.) accounted for 93.9 % of the number of grains, and the ten rarest types (*Arenga* spp., *Mangifera* spp., *Oroxylum indicum* Vent., *Barringtonia* spp., *Rhizophora* spp., T4, T6, T10, T12, T13) accounted for only 0.6%. The pollen grains of *Musa malaccensis* Ridley and *M. truncata* Ridley (cultivated *Musa* does not produce pollen) are rapidly broken down in guano and thus were not available for counting but field observations indicate that this genus is not of major importance to *E. spelaea*. No account was taken of the relative sizes of the pollen grains of the various species although they differ greatly; for example a *Parkia* polyad (counted here as one grain) is about 140 times the volume of an *Artocarpus* grain.

The percentage in the samples of pollen of seasonally flowering trees (e.g. *Bombax valetonii* Hochr., *Ceiba pentandra, Durio* spp., *Parkia* spp.,) and those which flowered in flushes (e.g. *Sonneratia alba, S. ovata* Backer) varied throughout the year and was closely correlated with observed flowering periods. However the percentage of pollen of those trees which flowered continually (e.g. *Cocos nucifera* L., *Duabanga grandiflora, Sonneratia caseolaris* (L.) Engl., probably *Artocarpus* spp.) also fluctuated, and this is presumably due to the feeding preferences of the bats at any given time.

Macroglossus minimus

This species is closely associated with the common mangrove genus *Sonneratia*, and indeed in West Malaysia it has never been recorded away from mangrove areas. At Rantau Panjang *S. caseolaris* was available as food throughout the year, whereas *S. alba* and *S. ovata* flowered in flushes and were jointly available for at least three quarters of the year. All chiropterophilous plants available in the vicinity were used as food to at least a limited extent. The less important sources were either rare or had short flowering seasons or both; *S. ovata* was rarely recorded because it has largely been eradicated by man at Rantau Panjang.

Macroglossus sobrinus

As with *M. minimus* this species is closely associated with a single genus of plants, in this case the bananas, *Musa* spp. However, here the correlation is even closer, for only one other type of pollen was found in the faeces, *Duabanga grandiflora*. Indeed *M. sobrinus* is in places probably entirely dependent upon *Musa malaccensis* and *M. truncata* Ridley or their hybrids. In a rubber estate near

Kajang about 20–30 *M. sobrinus* were apparently obtaining all their pollen requirements from about 50 trees of *Musa malaccensis*, but nectar requirements were supplemented from cultivated *Musa*. Cultivated *Musa* is used as a source of nectar only if wild species are in the vicinity, just as the proximity of *Sonneratia* species is necessary for *M. minimus* to visit cultivated *Musa*. Groves of cultivated *Musa* isolated from these two plant groups will only be visited by *E. spelaea*. *Musa violascens* Ridley, which has upright inflorescences, is bird pollinated and observations showed that it was not visited by *M. sobrinus* even when growing in close proximity to chiropterophilous *Musa* spp. with their pendulous inflorescences.

Feeding niche overlap

It is apparent that there is very little overlap in the feeding niches of the three species. There is frequently temporal separation of *E. spelaea* and *Macroglossus* when feeding: the most active feeding period for *Macroglossus* is within the first two hours after sunset but *E. spelaea* will often not reach the areas where *Macroglossus* is abundant until two hours after sunset due to the distance from their large colonial roosts. With the two *Macroglossus* species the only overlap is with the nectar of cultivated *Musa*, but the species are separated spatially, *M. minimus* being coastal and *M. sobrinus* inland. This is true not only in Malaysia but also in Thailand, Laos, Vietnam, Sumatra and Java. However, where *M. sobrinus* is absent, e.g. Borneo, Philippines, Sulawesi, *M. minimus* is found both in the mangroves and inland (Harrisson, 1966; Hill, 1966; Hill & Thonglongya, 1972; Lim & Heyneman, 1968; Medway, 1965; Phillips, 1967; Start, 1974; Tan, 1965; van Peenan, 1968).

Bat flowers

In a review of chiropterophily Faegri & van der Pijl (1966) tabulated those features they considered typical of "bat flowers", and this has formed the basis of later discussions on chiropterophily (e.g. Baker, 1970a, 1973; Procter & Yeo, 1973; Vogel, 1968–69). In the present study the following characteristics were examined: time of anthesis, colour, odour, flower structure, volume of nectar and pollen, position of inflorescence on the plant. It is apparent that previous generalizations about bat flowers were too sweeping. However, the universality of the features that characterize bat flowers is well illustrated by the fact that chiropterophilous plants from the Old World, where they are visited by Megachiroptera, attract Microchiroptera when they are transplanted to the New World, e.g. *Durio zibethinus* L. (Baker, 1970a) and *Musa* spp. (Walker, 1964). Conversely New World chiropterophilous plants transplanted to the Old World are visited there by Megachiroptera, e.g. *Agave angustifolia* Haw., and *Crescentia cujete* L., in Java (van der Pijl, 1936).

It has been found of value in this study to divide bat flowers into two groups:

Group I. Aseasonal flowering: each species with relatively small numbers of flowers per night but some flowers available continuously or for long periods; frequently growing gregariously. Three species of *Musa*, *Cocos nucifera*, *Arenga* spp., *Duabanga grandiflora*, *Sonneratia caseolaris*, also probably *Rhizophora* spp.

Group II. Flowering seasonally or in flushes: each species with great number of flowers per night (except *Sonneratia alba* and *S. ovata*); all plants of one species in one area flowering together; do not grow gregariously (except *S. alba* and *S. ovata* and plantations of other species). All other species (Table 1) except *Oroxylum indicum* which has characteristics of both groups, and *Artocarpus* species, T3, T4, T6, T10, T12, and T13 which remain unidentified to specific level.

In general *Macroglossus* species feed upon Group I plants and *E. spelaea* on Group II. However *E. spelaea* will readily turn to Group I if Group II plants are scarce or unavailable; indeed in monthly faecal samples taken from Gua Sanding (Perak) pollen of *S. caseolaris* was always abundant. It has been suggested that sequential flowering amongst seasonally flowering species may minimize competition between plants for pollinators (Frankie *et al.*, 1974a, b), but it may concentrate bats upon a single species during its flowering period and thus enhance the chances of cross-pollination.

Food sources other than flowers

In the faeces of the three species remains of arthropods (Insecta: Chelicerata–Acari) were found while *E. spelaea* faeces also contained plant material. It is likely that the majority of arthropods, most of which were very small (less than 1 mm long), were ingested accidentally. However it is possible that some fruit and some large insects (Lepidoptera) form a small part of the diet, liquid material being ingested and solid matter rejected as is common in Megachiroptera (van Someren, 1972; Walker, 1964; and pers. obs.).

ROLE AS POLLINATORS

Of the 31 types of plant listed in Table 1, eight cannot be identified even to the generic level and about these little more can be said. A list of the truly chiropterophilous plants of West Malaysia should probably not contain some of the remaining 23 types, e.g. *Rhizophora* species, but others should be added such as certain close relatives of species listed, e.g. other species of *Durio*, *Parkia*, *Eugenia*, and certain exotics, e.g. *Agave* spp., *Adansonia digitata*, *Crescentia cujete*.

That a flower is visited by bats does not mean that it is pollinated by them and certainly not that they are the major pollinating agents. In this study little work was done on the importance of bats as pollinators of specific plants but it is clear that the three species studied have the characteristics of potentially successful pollinators; for example they carry much pollen and move frequently from flower to flower. Also, many flowers visited are adapted both morphologically and biologically to visits from bats.

The flowers of many of the species listed were observed to be visited by potential pollinating agents other than bats, and it is clear that certain species such as *Cocos nucifera* and *Mangifera* spp. are not dependent upon bats for pollination. However *E. spelaea*, being a bat of great dispersive powers, may play an important role in their biology by disseminating their pollen widely. Others such as *Musa* spp., *Durio* species and *Parkia* species are probably dependent upon bats; other visitors, like sunbirds (Nectarinidae) or bees (Melaponidae), which may affect pollination, are probably of little biological consequence (Baker, 1973; Baker, Cruden & Baker, 1971). In summary, *E. spelaea* and the two *Macroglossus* spp. must play a significant role in the pollination of many of the plants listed in Table 1, most notably members of the families Musaceae, Bignoniaceae, Bombacaceae, Leguminosae, Myrtaceae and Sonneratiaceae.

A number of the chiropterophilous plants of West Malaysia are of considerable economic significance, foremost amongst these being *Durio zibethinus*, *Parkia* species and *Ceiba pentandra* (see Ashton, 1976). Further studies should be undertaken upon the importance of bats as pollinators of these plants: such studies should entail an examination of the rewards (i.e. the volume and nutritive value of nectar and pollen) they provide their animal visitors (Baker & Baker, 1975; Cruden, 1976) and also an examination of the breeding systems of the plants.

Currently both *E. spelaea* and *M. minimus* are threatened by man's activity, notably by the clearance of inland and mangrove forests, and by the quarrying of the limestone hills in which the great cave roosts are found. Whereas inland forest clearance encourages the spread of wild *Musa* species and thus possibly of *M. sobrinus*, it often means the replacement by monocultures of the diverse food sources necessary for *E. spelaea*. Batu Caves contain the only large colony of *E. spelaea* in Selangor state and the hill in which they are situated is being rapidly quarried. It is of interest, if depressing, to speculate upon the effect of the Caves' destruction and further forest clearance on the fruit-growing industry of this populous state.

ACKNOWLEDGEMENTS

We would like to thank Dr P. S. Ashton (UK) and Dr D. R. Wells (Malaysia) for much advice and encouragement. We are also most grateful to the following for assisting in numerous ways: Mr J. E. Hill (UK), Dr K. Jong (UK), Dr Kiew Bong Heang (Malaysia), Lord Medway (UK), Dr J. Muller (Holland),)Mr D Purcahse (Australia), Dr P. A. Racey (UK), Dr E. Soepadmo (Malaysia, Mrs. J. C. Start (UK), Dr G. Thanikaimoni (India). We are indebted to the University of Aberdeen for financial assistance, the University of Malaya for laboratory facilities, and to bodies of the Federal and State Governments in Malaysia for permission to conduct the research there.

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